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WEITERE INFORMATIONEN OK

Monday, May 23, 2011

Lactase persistence and quasi-pastoralism

One of the more interesting and well-documented events of recent human evolution is the rise of adult lactase persistence, which allows some of us to fully digest milk as adults. All mammalian young, including human, can digest the sugar lactose found in their mother's milk. Essential to this digestion is the enzyme lactase. However, mammals typically lose this ability after being weaned, as a regulatory genes turns off expression of the lactase gene. This loss of lactase production, and thus of lactose digestion, also occurs in most humans: most adults who consume milk don't digest most of the lactose due to insufficient lactase enzymes, and often develop digestive discomfort, a condition called lactose intolerance. However, at least once in Africa, once in Europe, and possibly in Arabia arose alleles in the regulatory gene that kept the lactase in production in adulthood. The spread of these new alleles probably occurred in cultures that already had domesticated milk-producing herds, the milk from which played a crucial role in their childrens' diets and indirectly in adult diets via fermentation (which, at some cost, convert some but not all of the lactose to molecules more readily digested by adults).

The lactase regulation mutation that spread most dramatically was in Europe, until by now it occurs in nearly the entire population of northwest European countries.

Modern frequency of lactase non-persistence as percent of the population in Europe.

This European lactase persistence allele soon came to be most concentrated along the Baltic and North Seas, what I call the core area of lactase persistence. Due to the heavy use of cattle in the core region, lactase persistence spread rapidly there, surpassing half the population by about 1500 BC.

The European lactase persistent populations played a substantial role in world history. The Baltic and North Sea coasts were the source of most of the cultures that conquered and divvied up the Western Roman Empire in the fourth through seventh centuries: Angles and Saxons (founded England), Ostrogoths and Lombards (Italy), Visigoths (Spain), Vandals (conquered north Africa), Frisians (the Low Countries)

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Nick Szabo

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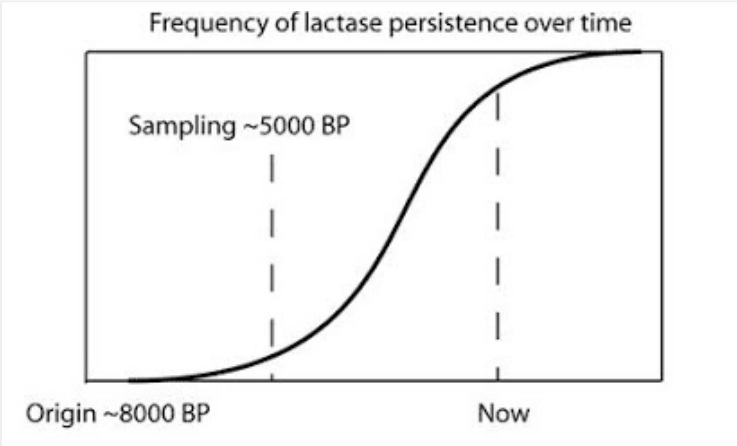
and Franks (France) among others. Later the lactase persistence core would produce the Vikings, who explored and conquered from Russia to North America and as far south as the Mediterranean, and the Normans, who invaded England, Sicly, and southern Italy led the Crusades among other exploits. Still later mostly lactase persistent populations would found the worldwide Portuguese, Spanish, French, Dutch and British empires and originate the agricultural and industrial revolutions.

Estimated spread of the European lactase persistence allele in the core region in northern Europe over time.



This was by no means the only gene evolving in the core. Indeed, the same cattle-heavy agriculture of northern Europe, probably originating in and migrating from central Europe, also gave rise to a great diversity of genes encoding cow milk proteins.

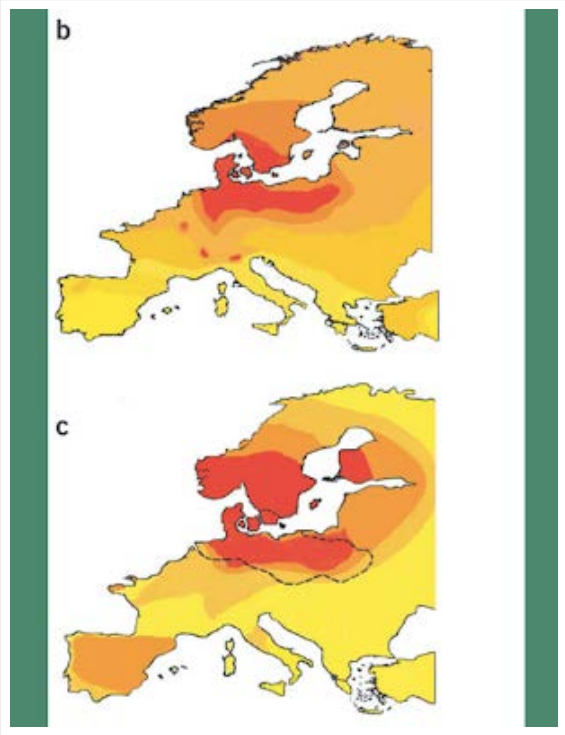
> We found substantial geographic coincidence between high diversity in cattle milk genes, locations of the European Neolithic cattle farming sites (>5,000 years ago) and present-day lactose tolerance in Europeans. This suggests a gene-culture coevolution between cattle and humans. [ref]

(b) diversity of cow milk protein alleles, (c) frequency of human lactase persistence.

Associated with the lactase persistence core was a unique system of agriculture I call quasi-pastoralism. It can be distinguished from the normal agriculture

Blog Archive

- ► 2018 (1)
- ► 2017 (3)
- ► 2016 (4)
- ► 2015 (3)
- ► 2014 (3)
- ► 2013 (3)
- ► 2012 (8)
- ▼ 2011 (12)
  - ► December (1)
  - ► July (1)
  - ► June (2)
  - ▼ May (2)
    - Bitcoin, what took ye so long?
    - Lactase persistence and quasi-pastoralism
  - ► February (2)
  - ► January (4)
- ► 2010 (9)
- ► 2009 (29)
- ► 2008 (55)
- ► 2007 (47)
- ► 2006 (130)
- ► 2005 (44)



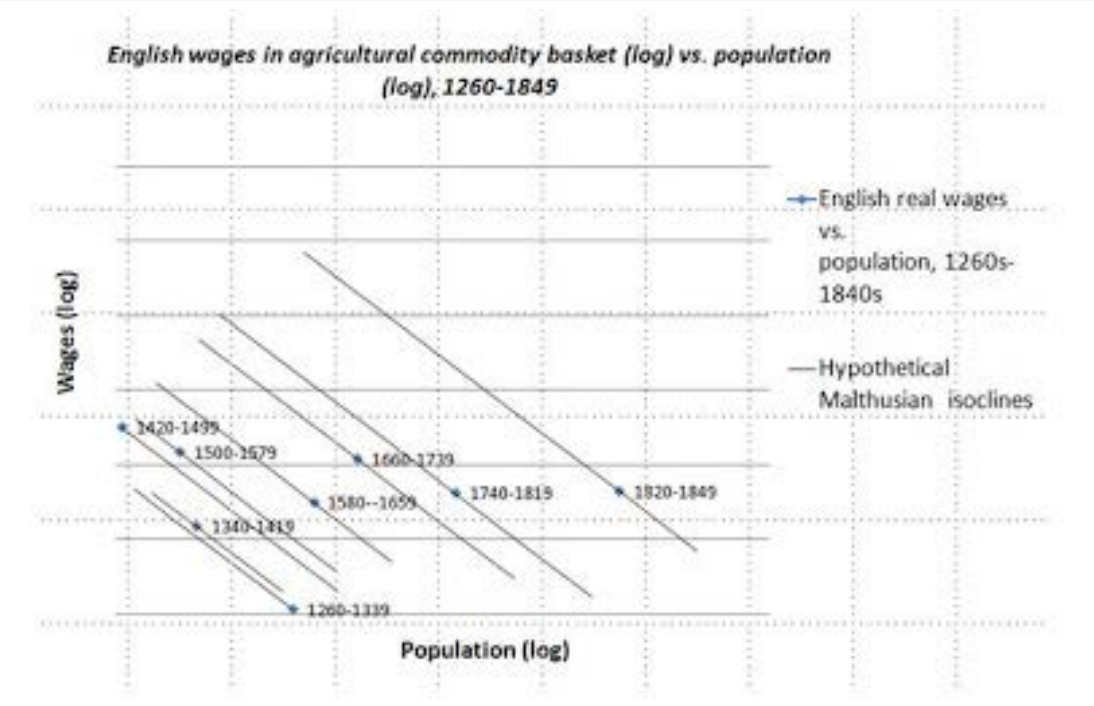
that was standard to civilization in southern Europe, the Middle East, and South and East Asia, in having more land given up to pasture and arable fodder crops than to arable food crops. Nearly all agriculture combined livestock with food crops, due to the crucial role of livestock in transporting otherwise rapidly depleted nutrients, especially nitrogen, from the hinterlands to the arable. However, as arable produces far more calories, and about as much protein, per acre, civilizations typically maximized their populations by converting as much of their land as possible to arable and putting almost all the arable to food crops instead of fodder, leaving only enough livestock for plowing and the occasional meat meal for the elite. Quasi-pastoral societies, on the other hand, devoted far more land to livestock and worked well where the adults could directly consume the milk.

Quasi-pastoralism can be distinguished from normal, i.e. nomadic, pastoralism in being stationary and having a substantial amount of land given over to arable crops, both food (for the people) and fodder (for the livestock). A precondition for quasi-pastoralism was the stationary bandit politics of civilization rather than the far more wasteful roving bandit politics of nomads.

Compared to the normal arable agriculture of the ancient civilizations, quasi-pastoralism lowered the costs of transporting food -- both food on hoof and, in more advanced quasi-pastoral societies such as late medieval England, food being transported by the greater proportion of draft animals. This increased the geographical extent of markets and thus the division of labor. England and the Low Countries, among other core areas, gave rise to regions that specialized in cheese, butter, wool, and meat of various kinds (fresh milk itself remained hard to transport until refrigeration). A greater population of draft animals also made grain and wood (for fuel and construction) cheaper to transport. With secure property rights, investments in agricultural capital could meet or exceed those in a normal arable society. The population of livestock had been mainly limited, especially in northern climates, by the poor pasture available in the winter and early spring. While hay -- the growth of fodder crops in the summer for storage and use in winter and spring -- is reported in the Roman Empire, the first known use of a substantial fraction of arable land for hay occurred in the cattle-heavy core in northern Europe.

England's unprecedented escape from the Malthusian trap (click to enlarge).

Hay, especially hay containing large proportions of nitrogen-rich vetch and clover, allowed livestock populations in the north to greatly increase. The heavy use of livestock made for a greater substitution of



animal for human labor on the farm as well as for transport and war, leading to more labor available for non-agricultural pursuits such as industry and war. The great population of livestock in turn provided more transport of nitrogen and other otherwise rapidly depleted nutrients from hinterlands and creek-flooded meadows to arable than in normal arable societies, leading to greater productivity of the arable that could as much as offset the substantial proportion of arable devoted to fodder. The result was that agricultural productivity by the 19th century was growing so rapidly that it outstripped even a rapidly growing population and Great Britain became the first country to escape from the Malthusian trap.

There are thus, in summary, deep connections between the co-evolution of milk protein in cows and lactase persistence in humans, the flow of nitrogen and other crucial nutrients from their sources to the fields, quasi-pastoralism with its stationary banditry and secure property rights, and the eventual agricultural and industrial revolutions of Britain, which we have just begun to explore.

Posted by Nick Szabo at 11:12 PM

13 comments:

Matt said...

A very compelling integration of previous posts.

When I've considered this, although it may not be essential to understanding your historical model, I've wondered if the choice not to use as much an arable land for food crops as opposed to fodder in the lactase core was motivated nutritional optimisation or by history.

That is, whether the quasi-pastoral model of the LP belt is a result (primarily or solely) either:

a - pure nutritional optimisation in an area (the lactase core area, and the North-Central European plain area generally) for which the Eastern Mediterranean legume/grain/vegetable fibre package suffered climatic inadequacies without clear substitutes.

or whether it is a contingent fact of history due to either

b - the chance emergence of a lactase persistence genotype in a particular time or context

or

c - for historical and cultural questions - by which I'm thinking that the adoption of a pastoralist mode of life early on, either for military or cultural or subsistence reasons, would have later path dependence that lead into a more quasi-pastoral form of agricultural, even though that wouldn't be "optimal" for increasing population. Particularly for this, I'm thinking of how cattle share decreases in the Western European areas during the dominance of the Roman Empire - see http://tinyurl.com/3w3wqca .

Perhaps you have implied or stated an answer on this one that I have missed. It seems that you are shading towards b here.

1:02 PM

nick said...

Good question, Matt. I doubt we have enough information yet for a definitive answer, but we know enough to shed some light on it.

Lactose persistence arose multiple times elsewhere in the world, so we know such mutations weren't astronomically improbable, but on the other hand lactase persistence appears not to have arisen independently in any of the many other pastoral regions of Eurasia besides perhaps Arabia, suggesting some luck involved.

DNA studies on burials now suggest that the European lactose persistence mutation originated in central Europe, not in the current core region. So the core region does not indicate origin so much as where the allele most out-propagated the competing alleles. The grain/legume (with livestock also important but secondary) model retained its dominance in southern Europe and other centers of early civilization. There is even a cline in England with Scotland more lactase persistent than than the English north or midlands, which in turn are more lactase persistent than southern England. This, alongside the north/south cline in continental Western Europe, suggests to me that milk for adults was especially beneficial in harsher winters, although that doesn't explain the lower levels of lactase persistence in northern Russia and Asia.

Figuring out when and by what stages northern Europe evolved from pastoralism to quasi-pastoralism may be a hopeless task. Though it's safe to say that the pre-Christian Germanic tribes, while far from being purely nomadic, had much more roving bandit to their societies than the Christian ones.

So the conversion (which also introduced other Latin institutions such as prose writing and Roman-derived law) was probably a very important step on the road from nomadic pastoralism to the advanced quasi-pastoralism that led to the agricultural revolution. Thereafter we see a great rise in the use of hay, a crucial innovation of advanced quasi-pastoralism, and a great elaboration of the northern European long-distance food trade, corresponding to the more secure property brought by Christian Germanic bandits who were far more stationary than the pagan Germanic ones. n.b. for those not familiar with the "bandit" terminology, Google ["Mancur Olson" bandit]. See also figure 3 of the link to the great Koepke et. al. paper you provided, showing a great increase in population density, especially in Central-Western Europe, starting not long after the conversion of the core region to Christianity.

But the northern bounds of the Roman Empire also suggest limitations to the process: they didn't succeed in conquering Scotland, nor the lands east of the Rhine or north of the Danube, and later succumbed to Germanic pastoralists, the whole of Western Europe moving towards the more roving banditry of the Germanic tribes and the Dark Ages, a pattern not reversed until all partly roving warriors like the Vikings and Magyars who plagued Europe were converted to a stationary lifestyle.

So perhaps the best short answer at least for now is, "it's complicated." :-) In other words some of all three of the factors you cite played a role.

4:10 PM

Daniel A. Nagy said...

Very interesting post, Nick! For a number of mostly personal reasons I have became interested in the cultures and history of Central Asia and their impact in the broader Eurasian context.
I do not, however, believe that there is a clear-cut difference between what you call pastoral and quasi-pastoral agricultures. In Central Asia, nomadic and settled peoples have always lived side-by-side with a relatively stable division of labor and trade inseparably connecting their economies. The political systems included both roving a stationary banditry at various times and areas. It is very interesting to research and observe the circumstances of phase transitions between these two principal systems of protection rackets and how the culture and economy adapted to them.

I certainly agree with you that lactose intolerance seems to be a very important constraint on the food economy. However, what was solved by means of genetic mutation in Europe was mostly solved by means of technology (based, as you write, on fermentation) in Central Asia and adjacent areas: kefir, yoghurt, ayran, qurut and kumis are just the most popular diary products specifically evolved to solve the problems you just mentioned.

Also, personal contact with those people made me realize that in many ways our modern society, while clearly a successor to settled agricultural societies, is getting closer to nomadic cultures and farther from its roots. For this reason, in Central Asia people with nomadic heritage have fewer problems adapting to modernity than those with a traditionally settled cultural heritage. Here are a few observations: in settled societies marriage is a complicated business deal of two families, while nomads have a far more relaxed (I would even say "liberal") attitude to sexual relationships, as cattle has been easier to divide than land. Our current social norms are much closer to those of nomads than to those of our settled ancestors a few hundred years ago. In North America, even housing is getting increasingly nomadic; a wooden-frame building put together from 2by4's and wrapped in Tyvek bears more semblance to a yurt from an engineering point of view than to the brick-and-mortar houses you'd find in Europe, albeit still mimicking the exterior appearance of the latter.

9:36 AM

nick said...

Great to read you again in the comments section, Daniel. Despite having many ancestors from interior Eurasia, I'm afraid I can't share any rosy view of its ancient ways. Almost all of the middle of the Eurasian continent sat at very "southwest" isoclines on the Malthusian graph, the opposite of where we in the modern developed world sit. This took the form of extemely low populatrion densities combined with somewhat higher standards of living (better diet) but more frequent violence. Quasi-pastoralists achieved many times the population density of interior Eurasia, and after hay and institutions of stationary society derived from Rome, probably hundreds of times the population density without most of the substantial diminution in the diet characteristic of grain-centered cultures. They thereby achieved levels of trade and urbanization unheard of in interior Eurasia and eventually in the industrial revolution exceeding those of grain cultures. Since there are plenty of good soils and climates for settled agriculture in central Eurasia, its extremely poor position on the Malthusian isocline must be based on the same pathology that caused the Greek and post-Roman Dark Ages, namely roving bandits. With so few geographical protections against the likes of Huns, Turks, Mongols, and yes even Magyars, nearly all of interior Eurasia lived in a permanent Dark Ages until modern times.

With rare exceptions -- the tribute capitals of conquerors like the Mongols, protectable regions like the Crimean penninsula, expensively secured trade towns along the Silk Road -- and later where the Rus (most likely) introduced hay and thus a degree of quasi-pastoralism to create Russia -- stationary cultures in central Eurasia were extremely small and fragile with practically no urbanization beyond the small village and the ephemeral tent fair. Ill protected and frequently raided by roving bandits. No stationary bandit society in interior Eurasia achieved there anything remotely close to what they achieved in Eastern Asia and Western Europe.

As for who is better adapted to modern life, that is a pretty open question. The main food adaptation problem we face is radically different: adapting to too much food and food our ancestors didn't eat. Both settled peoples and nomads lived with a small group their entire lives, so modern life with its Rolodexes or Facebook friends lists filled with hundreds of acquaintences who we haven't seen in years, (or thanks to the Internet never even met), is unlike practically all major traditional lifestyles.

12:20 PM

nick said...

errata:

"somewhat higher standards of living (better diet)" the comparison here is to ancient grain-centered socieities. The interior Eurasian diet was roughly comparable, perhaps slightly better in nutritional value than those of quasi-pastoralists.

"its extremely poor position on the Malthusian isocline" should be "the extremely poor position *of* its Malthusian isocline."

12:31 PM

Daniel A. Nagy said...

Nick, I think I also should have been more specific. My personal reasons have nothing to do with my ancestry; I have some business interests there and happened to make a few friends.

Of course, the main centers of civilization in Central Asia are the cities along the Silk Road between Urumqi and Istanbul. Their population numbers and amassed wealth were quite decent by medieval standards. The overall low population density is, in my view, mostly due to the shortage of water and the very extreme continental climate. Coastal regions on all continents tend to be much more densely populated than the middle. The destructive effects of roving banditry are, of course, not to be under-stated, but I would abstain from assigning a clear cause-effect relationship here.

When talking about settled and nomadic cultures, I was specifically referring to those in Central Asia: Persians, Tajiks and Uzbeks are typically settled peoples, while Kazakhs, Kyrgyz, Uyghurs and Mongols have been until very recently typically nomads.

Settled peoples and nomads have lived side by side for a very long time in Central Asia, and relied very much on each other. The popular narrative of nomads being simply barbaric parasites on cultured settled peoples is hugely over-simplified and fails to capture the economic dynamics of the Silk Road.

If there were no mutual dependence and one of these cultural templates were clearly superior, it would have simply won. Neither did, because they needed each other. For example, markets (bazaars) of settled peoples would not have worked as well as they did without the collectibles such as jewelry and rugs typically supplied by nomads. Wool and felt were also typically produced by nomads and I doubt that it was purely a comparative advantage issue.

Now, modern industrial and post-industrial social patterns *are* winning, but surprisingly, they are winning over former nomads first. To my profound surprise, the social segregation is not between native population and newcomers (or colonists or whatever the non-native population -- typically Russian-speakers -- is supposed to be called) or Muslims and non-Muslims, but between traditionally settled native peoples (such as Uzbeks and Tajiks) and everybody else. In today's Uzbekistan the cultural difference -- especially as far as economic activity is concerned -- between native Kazakhs and Uyghurs, whose great-grandparents lived in yurts, on one hand and Germans, Russians, Koreans, Ukrainians and Armenians whose grandparents or great-grandparents moved to Central Asia from thousands of kilometers away is almost negligible; they all speak perfect Russian, live in large cities and typically work in industry, services or education. They tend to hang out together and mixed marriages are frequent. Native settled peoples cling on to their traditional culture much more; they typically work in agriculture, in retail or in government and speak Russian as a second, foreign language if at all. Dating an Uzbek for a non-Uzbek would be difficult to begin with and would very quickly involve complications with their extended family. There are exceptions, of course, but this is the norm.

As for food, nomadic cuisine is mostly meat and pastry. Settled diet has remarkably less meat, but more fruit, vegetables and spice. But for at least the last 1000 years or so there has been very intensive exchange of food in bazaars. There is, however, and has always been a marked shortage of some micro-elements (such as iodine) in Central Asian diet, that we typically get from seafood.

4:50 PM

Daniel A. Nagy said...

I do not know (and have no idea how to find out) how much trade of food occurred on the timescale (order of 10 000 years) significant for human evolution of lactase persistence between steppe nomads and farmers in Central Asia, but I would guess that it pre-dated intensive trade along the Silk Road, because at times it might have made all the difference between life and death.

The rapid spread of lactase persistence among nomads (with the notable exception of Mongols) may also be attributed to the tradition of exogamy coupled with the obvious usefulness of the allele for them. At the same time, this same exogamy and the recessive nature of lactose intolerance might have prevented lactase persistence to become as ubiquitous as it is in North-Western Europe.

It should also be noted that periods of nomadic empires overrunning (and, due to roving bandit politics, overtaxing) settled peoples such as Hun and Mongol conquests were relatively short and infrequent (though dramatic enough to capture the imagination and imprint mostly false stereotypes). Much more typically, nomads lived at the mercy of their farmer neighbors precisely because of the latter's more efficient use of land. It would actually be an interesting research topic, what conditions triggered the coalescence of various nomadic tribes into conquering empires; I suspect that the folklore narrative of the emergence of exceptional leaders plays a far less significant role than the dynamics of good and failed harvests among neighboring farmers, market prices of livestock, etc. What kept nomadic lifestyle alive until very recently was not military superiority (which did not exist most of the time), but the flexibility afforded by mobility and the various ways in which it facilitated long-distance trade between farmers. In arid climates, it is sometimes a safer bet than farming.

2:03 AM

Anonymous said...

This is an amazing posting!

1:01 PM

Anonymous said...

Perhaps I am thick but what I am not understanding is why there is a wages-population isocline.

Are you saying that there is a fixed amount of resources and that they must be shared among the population, so with a larger population everyone gets less?

Secondly, how do populations move between the isocline? Is it the discovery of new energy sources?

1:11 PM

nick said...

Daniel, very informative comments. The settled cultures you cite seem to be primarily Iranian derived (with various nomads absorbed during some periods), with heavy traditional influence and often control of the Persian empire (located largely at the periphery, not the interior of Eurasia, and similar to Rome's control and influence over Western Europe). From eyeballing maps, the settled farming north of modern Iran seems to have been largely confined to narrow strips of irrigated fields along rivers. It seems to take the rich nutrients (not just water) provided by irrigation, and a very mild climate, to produce a farming region dense and productive enough

in the interior of central Asia to survive, to some extent, the depredations of neighboring roving bandits. But unlike the more geographically peripheral Sumer/Assyria/Babylon and Persia civilizations based on such irrigation, they weren't able to extend that influence to larger regions but rather came to be much more politically dominated by the neighboring nomadic cultures.

While the relatively lesser amounts of rain in much of the interior is thus a factor, by itself it would not prevent settled agriculture: it's easy to grow e.g. winter wheat without irrigation in such semi-arid climates if security is not a concern. But it doesn't give the productivity needed for a population sufficiently dense to survive roving bandits.

Exogamy is an interesting theory for why lactase persistence spread more slowly among the steppe nomads than in the regions of what is now Scandinavia, the Low Countries, and the British Isles (see maps above). But roving bandits may provide another explanation. What were the traditional animals used for milk on the steppe? My understanding is that horses, goats, and sheep were much more used and cattle much less compared to the lactase persistence core of northwestern Europe. I suggest this was for security reasons: cattle represent too large a capital investment in the very exposed nomadic societies of the steppes. Horses are easier to protect (they can run and escape, often carrying owners and possessions in the bargain, and as cavalry can help you defend) while sheep and goats are smaller and more readily dispersed and replaceable capital investments.

1:57 PM

nick said...

Anonymous (choose a handle, please, so we can distinguish the different anonymous participants, thanks):

Are you saying that there is a fixed amount of resources and that they must be shared among the population, so with a larger population everyone gets less?

Almost. What happens is, that at any given fixed level of technology and institutional arrangements, the most fertile land is generally already being farmed and so an extra person must get their food from less fertile farmland. So there are extra resources available but they are more expensive to use. For food that requires more labor per unit of nutrition, and so nutrition per capita thus declines. (Until recent centuries in the developed world, per capita nutrition can be treated as equivalent to per capita income for the vast majority of the population, as food constituted the great majority of expenditures).

Secondly, how do populations move between the isocline? Is it the discovery of new energy sources

New energy sources is one possibility, although in the epochs I'm describing it's largely agrarian capital investments (e.g. accumulating more cattle or building irrigation ditches) and innovations (e.g. hay, more or better use of nitrogen-fixing plants, property rights arrangements that are more secure or provide better incentives), or the decay or destruction of capital investments and the forgetting of innovations that moved the isocline "northeast" or "southwest" respectively over the long term. Over shorter periods, very large short-term fluctuations of the isocline (that swamped the effects of innovation over these short periods) were caused by weather, pests, and other variables impacting annual harvests. Wars could have a major temporary impact; their long-term impact on the isocline depended on how they influenced institutions.

2:18 PM

Beyond Anon said...

So, it seems that you are saying that at the margins, each extra unit of population reduces the resources (calories) available for everyone.

However, practically, those who have earlier claims to land and resources are less likely to experience declines in resource availability (at least where there are property rights).

So, an interesting question is: What lead to the notion of property rights? This did not seem to develop in China, for example, where the emperor could claim anyone else's property at will.

4:53 PM

nick said...

China had private tenure with fixed rents or taxes in most eras and areas, much like Japan and Western Europe. The main difference between China and Britain that I have surmised is that capital investments tended to occur at two extremes in China: within family farms and from large state bureaucracies. This also tended to be true in France which also lagged in the agricultural and early industrial revolutions. Whereas Britain with the enclosure-and-improvement movement found a happy medium, capital-intensive private farms employing wage labor (the forerunner of modern corporate farming). These achieved economies of scale and labor efficiencies that neither family farms nor larger political bureaucracies could achieve. This different outcome may derive from two factors: (1) the Chinese had more external security costs than Britain, motivating them to keep a tigher grip over land and food and increasing taxes, and (2) their property law may have been more rigid, suitable only for family farms or state bureaucracies and not much in between.

These are both very speculative conjectures though. Big caution: we actually know very little about the details of the historical Chinese legal systems. There is great uncertainty about them and various theorists have been all over the map ranging from calling the emperors proto-Maoists to portraying their system as a private property paradise. Both extremes are wrong except in certain narrow times and places, but alas nobody really knows what the reality is AFAIK. (If anybody knows a good study based on Chinese legal cases of the ancient Chinese property law, translated into English, I'd love to see it, but alas I've never encountered such a work).

The origins of property are lost in prehistory, as practically all agricultural societies had some form of it.

The flat ownership (what in English law we call fee simple), a.k.a. several property, system as opposed to "feudal" hierarchies of tenures (which range from rental-at-will to long-term tenures nearly indistinguishable from what we call "ownership") we get from Roman law. It was lost during the Middle Ages, and reemerged during the British agricultural revolution alongside the enclose-improvement movement. The hiearchical ("feudal") model was better suited to protecting units of land smaller than a state from warfare, but where security was provided by larger states or empires several property (where ideally everybody owns rather than rents) tends to work better. In between a common pattern was long-term leases with fixed rents, which isn't terribly different from what we understand as "ownership" of several property.

4:32 PM

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